

Thermoregulation in feeding baleen whales: Morphological and physiological evidence

John E. Heyning

Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, CA. 90007, USA

Abstract

Gray whales (*Eschrichtius robustus*) expose their immense oral cavities repeatedly to frigid waters when feeding. Morphological structures for heat conservation in the tongues of gray whales are described here in detail. Numerous individual countercurrent heat exchangers converge at the base of the tongue to form a bilateral pair of vascular bundles called the *lingual rete*. Temperature measurements taken from a live captive gray whale calf indicated that more heat could be lost through the blubber layer over the body than through the tongue, despite the fact that the tongue is far more vascularized and has much less insulation. Hence, these heat exchangers substantially reduce heat loss when these whales feed in cold waters. The evolution of these structures was a physiological prerequisite for baleen whale breeding.

Key words: mysticete, thermoregulation, countercurrent mechanism, *rete*, gray whale, tongue.

Introduction

The oceans and seas are energetically challenging environments for endotherms because water conducts heat away at approximately 25 times the rate of air. There are three primary mechanisms by which cetaceans regulate their body temperature. The first is through insulation, for which cetaceans rely on the subdermal layer of adipose tissue coined 'blubber' by early whalers. Second, is to regulate blood flow to the surface of the skin, especially through the extremities. All cetaceans have an extremely complex vascular system to achieve such regulation. Thirdly, the metabolic rate can be increased to generate more heat for the system. Whether or not any cetaceans have an elevated basal metabolic rate is controversial (e.g. Lavigne *et al.*, 1986; Kastings *et al.*, 1989; Kastings, 1991; Innes & Lavigne, 1991).

The insulating blubber often is considered an inert insulative covering. In reality, by varying blood flow, the insulative property of blubber can be bypassed and hence thermoregulation is quite dynamic. Many of the larger cetaceans have no trouble staying warm even in polar waters (Hokkanen, 1990); in fact, dumping heat could be more challenging under some conditions. Even for smaller species, there are times when certain organs must be actively cooled to prevent tissue damage. Because with any endotherm, a cetacean needs to avert excess heat loss and also regulate its core body temperature in relation to its metabolic rate and the ambient temperature (Parry, 1949).

The blubber effectively insulates the majority of the body surface and the countercurrent heat exchangers in the vascular system of the fins and flukes of whales and dolphins serve to conserve core body temperature. However, a critical anatomical region relating to thermoregulation was overlooked for decades. Baleen whales (suborder Mysticeti) have cavernous mouths to accommodate the large filtering surface comprised of baleen. Whereas, the blubber enshrouding the head provides suitable insulation when the mouth is closed, the inner surface of the mouth is highly vascularized and relatively uninsulated. Furthermore, most species of baleen whales feed in the cold waters of high latitudes. Therefore, feeding exposes the large surface area of the tongue to the cold polar and subpolar waters these whales inhabit.

Ryg and colleagues (1993) first noted that the oral cavity of feeding baleen whales represents a major surface for heat loss; however, they lamented that there were no measurements to quantify this loss. Small countercurrent heat exchangers have been described for the gums and palate of fin whales, *Balaenoptera physalus* (Utrecht, 1958). The narrow palate of the right whale has also been suggested as a site for heat dumping (Ford & Kraus, 1992) although Heyning, *et al.* (1993) noted that the palates of right whales lacked the

specializations necessary to serve as an important site of heat loss.

The purpose of this report is to provide: 1) more details of the previous study by Heyning & Mead (1997) on countercurrent heat exchangers in the oral cavity; 2) an overview of thermoregulation; 3) a context for the oral cavity of baleen whales, and 4) a comparative context among baleen whales to understand the distribution and evolution of these important structures.

Materials and Methods

Heyning & Mead (1997) dissected two freshly dead gray whale calves. The tongue of the smaller calf (LACM 88981; 3.98 m) was transversely sectioned at about 2 cm intervals and probes were inserted into the blood vessels to trace their course. The *in situ* architecture of the lingual rete of the larger calf (LACM 92044; 5.25 m) was revealed by superficial to deep dissections to observe the connection of this plexus to the cranial-cervico vascular system.

I measured the surface temperature of the tongue and the skin of the head and neck of a live gray whale calf (JJ) during a series of feedings. Temperature measurements were obtained using a Raynger PM model PM313tru remote thermal sensor held within 1 m of the target. Measurements were made when the calf briefly lifted its head out of the water at the beginning and the end of a feeding session. Each recording was based on several individual measurements made over a period of several seconds. Measurements were taken after most of the water dripped-off, but a thin sheen of water remaining upon the body surface. The temperature measurements from the neck region did not change from its initial reading until the animal re-submerged after at least 1 min of exposure to air. This suggested that any biases in measures from the wet surface area should be minor and apply equally to all measurements.

The first measurements were taken when the calf was about four months old. At this time the ambient water temperature was 19.5°C. A second series of measurements were taken when the calf was about eight months old in ambient water temperature of 12.5°C. In both temperature regimes, the relative temperature relationship between the ambient water, body surface, and tongue surface did not change further suggesting that measurement biases were minor.

Results and Discussion

Anatomical evidence

Walmsley (1938) and other early workers identified and clearly described the anatomical configuration

of countercurrent heat exchangers, yet were perplexed as to the function of these vascular bundles. The first author to ascribe a function to countercurrent heat exchangers in marine mammals was Parry (1949) who noted that by shunting arterial heat into the 'accompanying venules' that heat would be short-circuited back to the body core. Parry's (*op cit.*) observations were of the superficial vascular system along the entire body. Far more impressive countercurrent heat exchangers subsequently have been found associated with various extremities and organ systems.

Countercurrent heat exchangers function by conducting heat from warm arterial blood coming from the body core to cool venous blood typically draining the body surface (Scholander, 1958). This is accomplished by situating an artery traveling to the body surface adjacent to the veins returning from that cool extremity. The warm arterial blood transfers its heat by simple conduction to the adjacent cool venous blood. In this way, body warmth is re-circulated back to the body core *vis a vis* the venous blood prior to losing heat to the environment. The classic countercurrent heat exchangers consist of a central arteriole surrounded by a plexus of small venules. This architecture was coined the peri-arterial venous *retia* by Elsner *et al.* (1974), a term which best describes the complex architecture of this network of interwoven blood vessels.

The fins and flukes of whales and dolphins, essential for locomotion and manoeuvring, are potentially significant sites of heat loss in cold waters because they lack insulative blubber and have relatively large surface areas. Conversely, it has been observed that when a cetacean is held-out of water, these extremities overheat relative to the torso skin temperature because the animal attempts dump excess heat through its appendages (Elsner *et al.*, 1974).

Recent studies (see Pabst *et al.*, 1998 for a review) have demonstrated that countercurrent heat exchangers are responsible for cooling the testes to promote spermatogenesis or the ovaries to prevent hyperthermia in the fetus. Cool blood from the flukes *via* the lateral caudal arteries and blood from the lateral abdominal subcutaneous veins, which drain the dorsal fin, conjoin and then divide into a series of small veins forming a venous plexus in the region of the gonads.

Like most baleen whales, gray whales have relatively large mouths and migrate to cold waters for feeding during the summer. Heyning and Mead (1997) calculated that the surface area of tongue of a gray whale represents approximately 5% of the surface area of the body, excluding the extremities. Thus, the oral cavity should be an important region for thermoregulation. Notwithstanding feeding, theoretical calculations predict that the blubber

layer of gray whales should effectively insulate these whales even in cold polar waters (Hokkanen, 1990).

Scattered throughout the tongue Heyning and Mead (*op. cit.*) observed numerous individual countercurrent heat exchangers consisting of a single peri-arterial venous *retia*. These individual countercurrent heat exchangers are about 0.7 cm in diameter. These blood vessels are oriented in planes so that cool venous blood from the surface of the tongue flows posteriorly and ventrally towards the base of the tongue. Along the posterior-half of the base of the tongue these numerous individual countercurrent heat exchangers converge to form a bilateral pair of *lingual retia* each comprised of approximately 30 such heat exchangers organized into a close-knit vascular bundle.

In the 5.25-cm. calf dissected by Heyning and Mead (*op. cit.*), each of these *lingual retia* was over 1/10th the body length. The individual countercurrent heat exchangers extending well beyond these *retia*, all the way to the surface of the tongue. Thus, the *lingual retia* form, both relatively and absolutely, the largest countercurrent heat exchangers previously described in any endotherm (Scholander & Schevill, 1955; Scholander, 1958). At the base of the tongue, these heat exchanger *retia* curve dorsally and separate into numerous individual arteries and veins that connect to the external carotid artery and jugular vein, respectively.

The distinct unbranched section of the lingual artery is short, bifurcating into numerous small arteries just distal to the carotid artery. This tremendous proliferation of arteries just proximal to the lingual *rete* functionally increases the cross-sectional area of this vascular system and thereby increasing the surface area of the blood vessel walls. Both of these structural attributes would function to significantly slow blood flow in any single vessel, in so doing increasing the time available for the transfer of heat from arteries to veins. Theoretically, this should greatly enhance the efficiency of this countercurrent heat exchanger system.

Other arteries and veins were found parallel to, but not associated with, the lingual countercurrent heat exchangers. By shunting blood through these collateral vessels, a gray whale might dump a significant amount of heat over the large lingual surfaces during times of strenuous activity or as needed in the warmer waters of their winter breeding lagoons.

Because a mobile and dexterous tongue is needed to control water flow over the baleen, the tongue could not properly function if it were enveloped within thick, semi-rigid blubber, such as that encasing the body. Nonetheless, the outer surface of the tongue is invested with a diffuse layer of fatty

tissue about 2 cm thick in the calves we dissected. A similar, but even more distinct, enveloping fatty layer of the tongue is clearly visible in a transverse section of the tongue of the obligatory Arctic species, the bowhead whale (*Balaena mysticetus*) (see Haldiman & Tarpley, 1993; Fig.4.17B). This outer layer of adipose tissue could be functionally analogous to the blubber layer of the body, providing at least some insulation for the tongue.

Physiological evidence

Heat is the form of energy that is transferred into or out of a body as a result of a temperature differential (Bartholomew, 1982). Thus, skin surface temperature relative to ambient temperature is a good indicator of heat loss to the environment and can identify regional heterothermy (e.g. Irving & Krog, 1955).

When JJ, the gray whale calf, first opened its mouth to suckle on a feeding tube, the surface of the tongue was 1.5 to 3°C above the temperature of the skin (21°C) on the dorsum of the head and neck region. After about one min of suckling, with the oral cavity only slightly open to the water, the surface temperature of the tongue dropped to 0.5°C above the ambient water temperature, now well below the temperature of the skin. This final 0.5°C temperature differential between the tongue and the water indicates that little heat is conducted out of the tongue. All temperature measurements were taken when the animal briefly raised its head out of the water during feeding bouts; therefore these measurements are not influenced directly by either water flow convection or boundary layer effects. Therefore, the drop in temperature on the surface of the tongue was a result of recirculating heat back to the body core *via* the lingual countercurrent heat exchanger. The core body temperature of a gray whale is 36.5°C (Morrison, 1962) similar to the 35–36°C core temperature of the closely related balaenopterid whales (Brodie & Paasche, 1985).

Results show that the temperature of the tongue initially dropped while feeding. This finding at first appears to be counterintuitive (e.g. Heath, 1998). To understand this initial drop in temperature, an understanding of the dynamics of thermoregulation is important. If an extremity with a countercurrent heat exchanger is in a warm environment, the blood in that extremity will be warm and the countercurrent heat exchanger has little impact on heat flow. This is the condition when the whale's mouth is closed and the insulating blubber of the head surrounds the oral cavity. However, when that extremity is exposed to a cold environment, the countercurrent heat exchanger cannot retain the heat already in the extremity, nonetheless it does serve to prevent further heat loss by recirculating

heat back to the body core. This is exactly what happens when the whale opens its mouth to feed and instantaneously exposes the warm tongue to the cold polar waters. Initially, the heat within the tongue is lost to the environment, but a continual heat loss is prevented by the countercurrent heat exchangers (Heyning & Mead, 1998). This prediction is in total congruence with our temperature measurements. Theoretically, without these countercurrent heat exchangers, the highly vascular tongue should have registered surface temperatures far greater than ambient, reflecting an endless heat loss during feeding.

Scholander & Schevill (1955) recognized two ways that the vascular system can reduce heat loss through the body surface, especially the extremities. The first is to employ countercurrent heat exchangers as discussed above. The second is to restrict the flow of blood to the skin by either reducing blood volume and/or slowing the rate of blood flow. Either of the latter results in a blanching of the skin due to the reduced amount of blood in the surface capillaries. During my measurements, the vivid pink color of the lightly pigmented tongue did not change noticeably. This pink color is a result of a rich profusion of blood throughout the tongue's capillaries. This implied that the animal was not merely constricting blood flow to the tongue when the mouth is opened as a mechanism to conserve heat.

Countercurrent heat exchangers in other mysticetes

Right whales and bowheads (balaenidae) possess exceptionally large tongues and mouths. The tongues of right whales have yet to be dissected to determine their presence or absence of countercurrent heat exchangers. Nonetheless, there is an undescribed countercurrent heat exchanger *rete* located within the mandibular foramen of bowheads (*Balaena mysticetus*) adjacent to the mandibular nerve as seen in Pfeiffer & Kinkead (1990, Fig. 1). This finding is reasonable based on the anatomy and ecology of this species. Along with their close kin the right whales, bowheads have a greatly enlarged lower lip that forms the lateral wall to the elongate array of baleen plates. This lower lip is vascularized by the mandibular artery. Bowheads employ a skim feeding technique similar to that of right whales. During skim feeding the mouth is held open to allow a constant flow of water through the filtering baleen plates. Such feeding exposes both sides of the immense lower lip to the cold polar waters these whales inhabit. A countercurrent heat in the mandible would function to reduce heat loss during feeding.

Heyning (1997) previously observed countercurrent heat exchanger within the tongue of an adult

female pygmy right whale (neobalenidae: *Caperea marginata*). There were five longitudinally-oriented countercurrent heat exchangers located deep along the midline of the tongue arranged in dorsal and ventral bilateral pairs and a single central artery. Each vascular bundle was approximately 1 cm in diameter. These arteries lost their association with the veins at the posterior base of the tongue. Because this observation did not occur until the finale of the tongue dissection, no more details could be gleaned from that animal.

The rorqual whales (balaenopteridae) engulf large volumes of water into their cavernous oral pouch, the *caven ventrale*, during feeding (Lambertson, 1983). Slijper (1936:157) illustrated the blood vessel pattern in a fetal minke whale (*Balaenoptera acutorostrata*) and depicted a large rete just ventral to the basicranium. This developing rete is in the exact anatomical region of the lingual countercurrent heat changer in the gray whale. Unfortunately, Slijper's text does not provide details of this *rete*. In addition, Carte & MacAlister (1869) mentioned that in the young minke whale they dissected that the veins of the tongue 'formed a plexus in the raphae near its base which terminated in the great jugular vein' (*op. cit.* 232).

In conclusion, all species of baleen whales have relatively large mouths and most species feed in the cold waters of the higher latitudes. Therefore, the oral cavities of all species of baleen whales should be examined in detail to determine the presence or absence of similar thermoregulatory structures because all baleen whales are likely to have evolved morphological structures that prevent heat loss during feeding. Such investigations need not be restricted to baleen whales. Walmsley (1938: Plate 36) presents a photograph of the cross-section through the mandibular canal of a sperm whale. The vascular architecture is that of a classic countercurrent heat exchanger similar to that found within the bowhead.

The abovementioned review of the anatomical literature revealed that countercurrent heat exchangers in the mouths of baleen whales could be a universal feature, although these vascular structures have never been identified. These findings strengthen the implication that for all baleen whales; the mouth is a crucial site for the regulation of body temperature during filtration of their prey. If all baleen whales possess lingual retes, it is most likely that these structures evolved in the common ancestor to all living mysticetes. Thus, the development of countercurrent heat exchangers within the mouths of baleen whales is probably as important as the development of filtering baleen in the evolution of mysticetes. It is these structures that have physiologically allowed these endotherms to exploit the high productivity of colder waters.

Future Studies

Measurements taken of skin temperature relative to ambient temperature provided a rough index of heat loss to the environment via conduction. The technique of thermal imaging uses this concept to provide a graphically rich, *albeit* qualitative, depiction of relative heat loss over a wider anatomical area. The use of such imaging could identify specific thermal windows on the animals not evident from simple point measurements. To quantify this heat loss, a device such as a heat flux transducer is required. The use of thermal imaging and a heat flux transducer in the future will provide a more detailed understanding of thermoregulation in cetaceans.

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